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STUDIES OF THE *LEPIDAPLOA* COMPLEX (VERNONIEAE: ASTERACEAE). I. THE GENUS *STENOCEPHALUM* SCH. BIP.

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Abstract.—The genus *Stenocephalum* Schultz-Bip. is resurrected for a group of five tropical American species related to the genus *Lepidaploa.* The two genera differ from *Vernonia* and are like each other in the form of their lophate pollen with "rhizomatous" columellae under the crests. The resurrected genus is distinguished structurally and functionally from *Lepidaploa* by fewer flowers in the heads. The surface of the pollen also has more numerous areolae, and the bases of the styles usually lack a node.

The establishment of a series of reliable and useful phyletic generic concepts in the tribe Vernonieae has already progressed considerably from the traditional core concept of Bentham and Hooker (1873) and Hoffmann (1890–94) that had numerous segregates based primarily on pappus variations. A major advance was that of Jones (1977) in recognizing basic differences in chemistry and chromosome number between New and Old World groups. Within the broad hemispheric groups are many genera, some of which have already been recognized in the traditional treatments, while others still reside in the synonymy of *Vernonia.* The present series of studies is aimed at the restoration or naming as new of many of the genera of the *Lepidaploa* complex that have been placed in the genus *Vernonia.*

The paleotropical elements of the tribe are phyletically remote from typical *Vernonia* in eastern North America, and are thus more easily justified at the generic level on the basis of the Jones' (1977) results. Some such genera recently resurrected include *Distephanus* Cass. and *Gymnanthemum* Cass. (Robinson and Kahn 1986), with the former not even fitting the broad concept of *Vernonia.* The neotropical elements fall into the same broad chemical and cytological group as typical *Vernonia,* but they also require segregation to a degree exceeding that found in the traditional tribal concepts. Many of the necessary additional segregates such as *Critoniopsis* Sch. Bip. (Robinson 1980) are at least as phyletically distinct as traditional genera like *Piptocarpa* R. Br. and *Pollalesta* H.B.K. Many small segregates remain to be recognized, but the largest number of neotropical species involved belong to the *Lepidaploa* group. Six genera, *Lepidaploa* (Cass.) Cass., *Stenocephalum* Sch. Bip., and four as yet unnamed, are to be treated in a series of studies of which the present resurrection of *Stenocephalum* is the first.

Significant Characters

Number of flowers in the head.—In the series of five genera, *Stenocephalum* Schultz-Bip. is notable for the comparative accuracy of delimitation at the time it was first published (Schultz-Bipontinus 1863). The paper in which the genus was described dealt mostly with genera with reduced numbers of flowers in the heads such as *Lychnophora* Mart. and *Eremanthus* Less. The reduced number of flowers appears to have been the

primary reason Schultz (1863) elevated *Stenocephalum* to generic level while leaving related forms in *Vernonia*. No phyletic considerations were evident in the work of Schultz, and the reduced number of flowers seems to have been regarded as a violation of the limits of *Vernonia*. *Stenocephalum* was relegated to the level of a section in *Vernonia* by Baker (1873) and has remained under the latter genus until the present. It was made a subsection by Jones (1979).

The present concept of *Stenocephalum* is more refined, and the relationship to other groups is now more evident. Even though the genus has no close relationship to the Lychnophorinae, the number of flowers in the head remains one of the most important characters in the delimitation of the genus. The heads contain usually 4–7 flowers, and rarely as many as 10. The characteristic number is lower than that in any of the other members of the *Lepidaploa* complex and moreover is reduced in proportion to the total of 15–22 involucral bracts in the heads. The reduction results in a lower proportion of flowers in four of the five species of *Stenocephalum* than the ⅖ to ½ ratio seen in most of *Lepidaploa*. The other exceptions in the group all have much larger numbers of both flowers and bracts. The ratio clearly distinguishes *Stenocephalum* from typical *Vernonia* which has more flowers and nearly equal numbers of bracts and flowers in the heads.

The reduced number of flowers in the head prevents some of the types of floral displays most common in the Vernonieae. In many members of the tribe the peripheral flowers spread in a manner resembling rays, a feature particularly notable in typical *Vernonia* and *Stokesia*. In *Centratherum* and some species like *Vernonia santosii* H. Robins. the zone of peripheral flowers is differentiated by maturing while the inner flowers remain unopened. The inner flowers open on another day with a distinctly unraylike appearance. These strategies are difficult if not impossible in the smaller heads of *Stenocephalum*, and in many cases the flowering heads are very unimpressive. Only *S. tragiaefolium* seems to furnish a notable floral display, caused by the massed effect of the whole inflorescence. One assumes that the limited floral presentation would have some effect on attraction of pollinators, but field observations remain to be made.

Disposition of heads.—The genus *Stenocephalum* consists entirely of species that have sessile heads at the nodes. The cymose structure is basically like that of *Lepidaploa* with none of the pedicellate modifications of the heads seen in either of the related unnamed genera. The heads may be isolated at separate, rather remote nodes as in the type species *S. apiculatum* or *S. jucundum*, clustered on short lateral branches as in *S. megapotamicum*, or more closely massed in a terminal inflorescence as in *S. tragiaefolium*. The variation of disposition of heads in the genus seems to be a significant factor in speciation. The two species, *S. apiculatum* and *S. jucundum*, that show similar displays have nearly complete geographical isolation.

Style base.—As noted in the study of *Distephanus* (Robinson and Kahn 1986), stylar nodes are widely distributed in the neotropical Vernonieae. Stylar nodes are particularly characteristic of *Lepidaploa*, often being quite marked as disc-like extensions at the base of the style just above the nectary. The node is lacking, however, in one related group that has previously been placed in *Vernonia* series *Buddleiifoliae*, and it is also poorly developed or lacking in the genus *Stenocephalum*. While most species have no node, a hint of basal differentiation is seen in some *S. megapolitanum* and a small but distinct basal rim is seen in *S. tragiaefolium*.

Achene structure.—The carpopodium of *Stenocephalum* was mentioned by Schultz (1863) as being large. The size is not unusual in the Vernonieae but the structure is uniform for all five species. The shape is short-cylindrical except for the rounding of the

basal margins. The upper edge of the differentiated structure is only slightly irregular at or below the level of the lowest setulae.

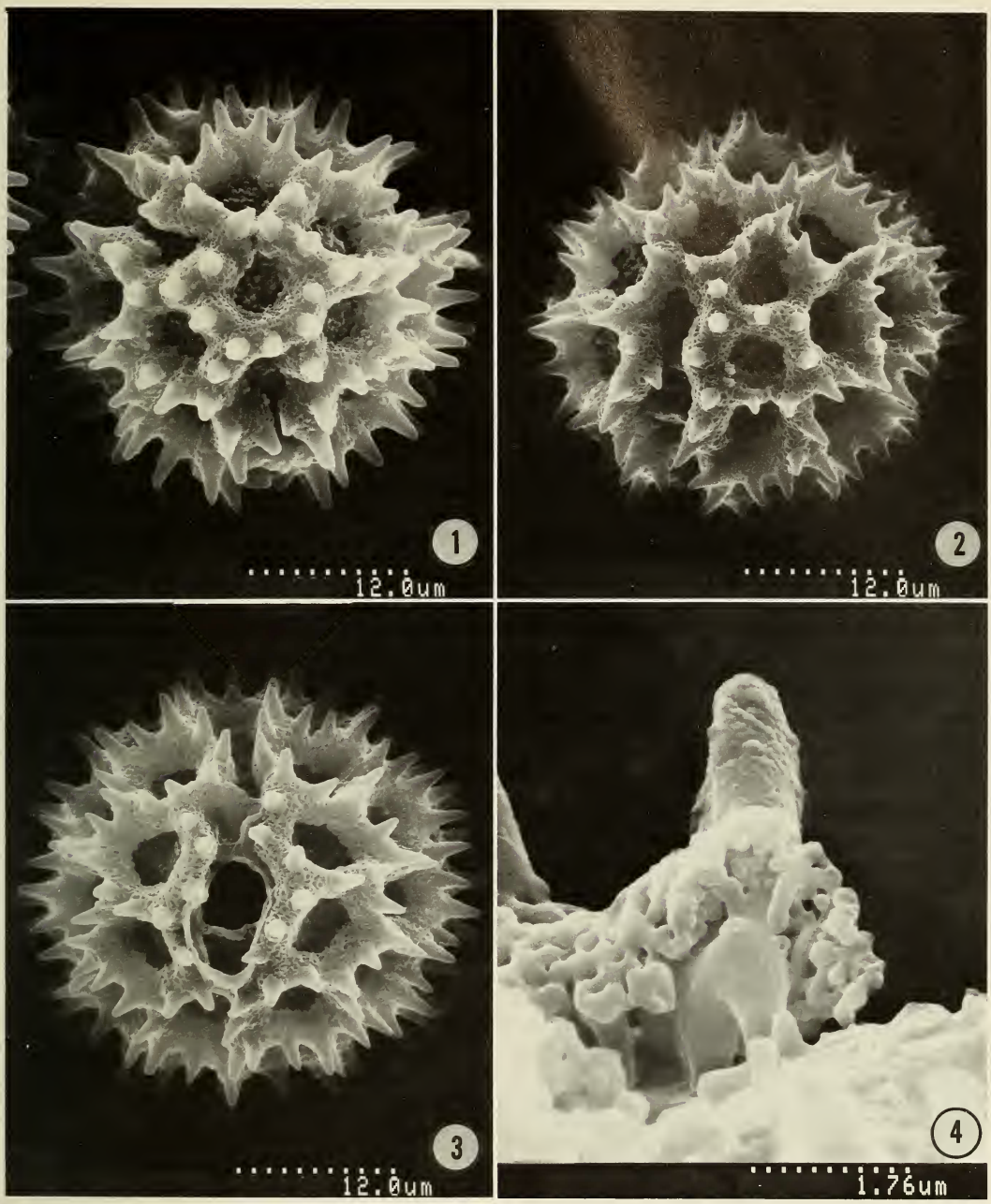
In contrast to the carpopodium, the achene wall structure in *Stenocephalum* varies extensively in setulosity and form of surface cells. The setulae seem characteristically somewhat contorted and uneven at the tips. One of the cells may project far beyond the other, or some setulae may be uniseriate from at or near the base. The ribs seem most prominent in *S. jucundum, S. megapotanicum* and *S. hystrix* where they stand out from the surface and separate the setulose areas into distinct bands. The ribs are weaker and the setulae more densely cover the surface in *S. apiculatum* and *S. tragiaefolium.* The ribs are particularly weak in the latter species and occasionally there are less than ten. In the type species, *S. apiculatum,* the cells of the intercostal region seem lax with weak walls that are scarcely observable under the microscope. The cells are most readily noticeable by the manner that they peel away with their imbedded setular bases from the thicker-walled elongate cells below. There are no other differentiated cells evident in this surface. The Central American and northern South American *S. jucundum* has surface cells that are similar to those of the type but they are much firmer and more easily seen. The three remaining species are seen to have thicker-walled elongate cells in immediate connection with the setular bases. All three species show islands of differentiated idioblasts with cells occurring singly or in a series of two to three. The latter pattern is one also seen in many species of *Lepidaploa.*

Pollen. — All members of the genus *Stenocephalum* show uniformity in their pollen and its general features differ only in details of areolation. The grains are of the type redefined here as *Lepidaploa*-type with the ridges of the lophate grains subtended by a horizontal "rhizome." The whole structure seems to easily peel away from the footlayer (Fig. 4). The grains of the type species shown (Figs. 1–4) differ from other *Lepidaploa* type pollens in the height of the crests and the exposure of the basal columellae, but the differences are ones of degree.

In form of areolation all the grains fall generally in the C-type which has areoles at the poles. The structure is unlike the C-type of *Lepidaploa,* however, in the extra number of areolae in the intercolpar region (Figs. 1–3). Observations under the light microscope indicate that none of the other species are as extreme in the number of areolae as the type species that is shown, but all have at least some extra, there often being three across the intercolpar region. The higher number of areolae and the presence of polar areolae is a combination unknown in *Lepidaploa.*

Relationship of *Stenocephalum*

The form of the pollen in *Stenocephalum* clearly indicates a phyletic position near *Lepidaploa.* This is advanced over the more primitive pollen type seen in such genera as *Stokesia* where the basal columellae each reach the footlayer individually. The presence of a trace of stylar node in *S. tragiaefolium* and the presence of idioblasts on the surface of the achene in three species of *Stenocephalum* also indicate a position close to *Lepidaploa.* The positions of the heads can also be interpreted as an seriately innovating cyme as in *Lepidaploa.* Nevertheless, the species potentially closest to the outgroup, *S. tragiaefolium* already shows some increase in the number of areolae on the pollen grains and already has the number of flowers in the head reduced to the point where the whole inflorescence is needed for floral display. Within *Lepidaploa* there is no species that seems particularly close to *Stenocephalum.* A species of the general *Lepidaploa* relationship that was initially thought to be related to *Stenocephalum, Vernonia regis* H. Robins., has enough flowers to fall completely within the *Lepidaploa* flower/bract ratio, a carpopodium on the achene with a more conical shape, much denser and straighter setulae on the achene



Figs. 1–4. Pollen of *Stenocephalum apiculatum* (Martius in DC.) Schultz-Bip. 1–3, dotted lines = 12 μm; 4, dotted line = 1.76 μm. 1, Polar view showing polar areole; 2, Oblique view showing half of intercolpus with complete median transverse row of three areoles; 3, Colpar view; 4, Broken section of crest showing details of "rhizomatous" columellae and attachment of perforated tectum.

with more equal tips, a well-developed node at the base of the style, and type-B pollen.

Stenocephalum Schultz-Bip.

Stenocephalum Schultz-Bip., Pollichia 20/21:385. 1863, type *Vernonia apiculata* Mart. ex DC.

Vernonia sect. *Stenocephalum* (Schultz-Bip.) Baker in Mart., Fl. Bras. 6(2):25. 1873.

Vernonia subsect. *Stenocephalum* (Schultz-Bip.) S. B. Jones, Rhodora 81:437. 1979.

Plants herbaceous, perennial, erect to 0.3–1.0 m tall, with little or no vegetative branching above the base. Leaves linear to broadly oblong, ovate or obovate, discolorous, dark green and densely to evanescently pilose above, pale tomentose below. Inflorescence cymose, heads single or grouped at primary nodes or densely clustered on lateral branches. Heads cylindrical; involucral bracts ca. 15–22 in 3–4 graduated series, with pungent usually narrowly acuminate tips (short cuspidate in some *S. megapotamicum*), slightly to distinctly recurved; flowers 4–7(–10) in a head; corollas lavender, with or without hairs at tips of lobes; anther thecae having shields of median endothecial cells variously radial or looped with multiple nodes, anther appendage glabrous; style base without or with only slight node. Achenes with ten ribs weakly to strongly developed, intercostal surface with surface of lax cells or with firmer cells intermixed with some idioblast clusters; setulae appearing evenly distributed in species with weak ribs, otherwise restricted between ribs, with often unequal and contorted tips, rarely uniseriate from base; carpopodium short-cylindrical, rounded only at basal margin; pappus of short outer squamellae and numerous inner capillary bristles. Pollen grains (40–)45–48(–50) μm in fluid, distinctly lophate with "rhizomatous" columellar structure under crests, exine easily stripping away from footlayer, lophate pattern of general C-type with polar areoles but differing by extra intercolpar areoles (up to 9).

Key to the Species of *Stenocephalum*

1. Cauline and primary branch leaves broadly ovate to obovate, distinctly narrowed at base 2
2. Heads laxly disposed along stems and branches, usually solitary in or near axils; leaves ovate (Central America, N. South America) ..... *S. jucundum*
2. Heads congested near apex of plant; leaves mostly obovate (Brazil) ..... *S. tragiaefolium*
1. Cauline leaves narrowly oblong with broadened bases or linear throughout, broader bladed leaves restricted to basal rosette 3
3. Cauline leaves linear throughout, narrow at base (Paraguay) .. *S. hystrix*
3. Cauline leaves linear to oblong with oblong or broadened bases 4
4. Inflorescence laxly branched with heads mostly solitary in successive axils; involucral bracts ca. 20, with narrowly acuminate tips; flowers ca. 4 in a head (Brazil, Venezuela) ..... *S. apiculatum*
4. Inflorescence often profusely branched with heads distinctly clustered in axils or on short branchlets; involucral bracts ca. 15, with shortly acuminate or cuspidate tips; flowers ca. 6–7 in a head (Argentina, Brazil, Paraguay, Uruguay) ..... *S. megapotamicum*

The species of *Stenocephalum* recognized in this study are as follows:

Stenocephalum apiculatum
(Martius in DC.) Schultz-Bip.
Figs. 1–4

Vernonia apiculata Martius in DC., Prodr. 5:51. 1836. *Vernonia monticola* Martius in DC., Prodr. 5:18. 1836. *Stenocephalum monticola* (Martius in DC.) Schultz-Bip., Pollichia 20/21:386. 1863. *Stenocephalum apiculatum* (Martius in DC.) Schultz-Bip., Pollichia 20/21:387. 1863.

The species is almost completely restricted to Brazil, but one specimen seen in this study from Venezuela seems to be this species [Bolivar: Rio Villacda (Rio Auyacda). Jan 6, 1956. *Wurdack & Monachino 41144,* US].

Stenocephalum hystrix
(Chodat) H. Robinson, comb. nov.

Vernonia hystrix Chodat, Bull. Herb. Boiss. ser. 11. 2:298. 1902.

Stenocephalum jucundum (Gleason)
H. Robinson, comb. nov.

Vernonia jucunda Gleason, Bull Torrey Bot. Club 46:248. 1919. *Vernonia spinulosa* Gleason, Bull. Torrey Bot. Club 52:188. 1925. *Vernonia llanorum* Badillo, Bol. Soc. Venez. Cienc. Nat. 10:218. 1946.

Gleason (1925) distinguished his Venezuelan species from the Central American entity by the narrower branch leaves, but his description indicated that the type had lost most of its leaves. The slight tendency that has been seen for the distal leaves to be narrower does not seem to justify separate specific rank. The picture has been complicated by the presence in southeastern Venezuela of the specimen mentioned above that has been determined here as the Brazilian *S. apiculatum.*

Stenocephalum megapotamicum
(Spreng.) Schultz-Bip.

Vernonia megapotamica Spreng., Syst. Veg. 3:437. 1826. *Vernonia megapotamica* var. *brevifolia* DC., Prodr. 5:51. 1836. *Vernonia megapotamica* var. *melanotrichia* DC., Prodr. 5:51. 1836. *Stenocephalum brevifolium* (DC.) Schultz-Bip., Pollichia 20/21:387. 1863. *Stenocephalum megapotamicum* (Spreng.) Schultz-Bip., Pollichia 20/21:388.1863. *Stenocephalum melanotrichium* (DC.) Schultz-Bip., Pollichia 20/21:388. 1863. *Stenocephalum penicillatum* Schultz-Bip., Pollichia 20/21:389. 1863. *Stenocephalum hexanthum* Schultz-Bip., Pollichia 20/21:390. 1863. *Vernonia hexantha* (Schultz-Bip.) Baker in Mart., Fl. Bras. 6(2):27. 1873.

Stenocephalum tragiaefolium
(DC.) Schultz-Bip.

Vernonia tragiaefolia DC., Prodr. 5:60. 1836. *Stenocephalum tragiaefolium* (DC.) Schultz-Bip., Pollichia 20/21:389. 1863. *Vernonia interjecta* Baker in Mart.?, Fl. Bras. 6(2):28. 1973.

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